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Chapter

The Response of Maize Physiology under Salinity Stress and Its Coping Strategies

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Abstract

Maize is a cross-pollinated, polymorphic plant in nature. It is commonly a moderately salt-sensitive crop. Salinity stress is the main abiotic factor that arrests the physiological characteristics and plant growth of a maize plant. It causes the osmotic effect, associated with an increase in phytotoxic ions, oxidative stress by increased reactive oxygen species (ROS) production, and ionic effect in the cytosol. These salinity effects hinder the maize plant's physiological processes such as respiration, photosynthesis, transpiration, stomatal functioning, hormone regulation, and functioning, seed germination, and dormancy and water relation with plants and ultimately reduce the plant growth and yield. However, the physiology of maize subjected to salinity shows various responses that depend on the genetic responses and growth stages. Maize plant undergoes many physiological changes and adapts some mechanism internally to cope with salinity stress. Numerous mitigating strategies such as application of chemicals, application of plant growth-promoting rhizobacteria (PGPR), application of hormones, and use of genetic and molecular techniques are used to handle salinity. This chapter will cover the effect of salinity on maize growth, its physiology, and physiological adaptations of maize plants with management strategies.

Keywords: *Zea mays* L., salinity, physiology, genetic and molecular techniques, antioxidants

1. Introduction

Soils with an excessive amount of soluble salts or exchangeable sodium in the root zone are termed salt-affected soils. Owing to limited rainfall and high evapotranspiration demand, coupled with poor soil and water management practices, salt stress has become a serious threat to crop production in arid and semi-arid regions of the world [1, 2]. Although the general perception is that salinization only occurs in arid and semi-arid regions, no climatic zone is free from this problem [3]. More than 800 million hectares of land worldwide is affected by either salinity (397 million hectares) or sodicity (434 million hectares) [4–6].

Maize (*Zea mays* L.) is the third most important cereal crop after rice and wheat and is grown under a wide spectrum of soil and climatic conditions. It is an important C4 plant from the *Poaceae* family and is moderately sensitive to salt stress;

nonetheless, wide intraspecific genetic variation for salt resistance exists in maize. According to the biphasic model of salinity-induced growth reduction [7], osmotic stress during the first phase and ion toxicity during the second phase are responsible for reduced growth in cereals, specifically wheat. The same model for salinity-induced growth reduction in maize was confirmed by [8], but ion toxicity and the associated growth reduction can occur, to a small extent, in the first phase in maize. The sensitivity of maize to salinity is associated with higher accretion of Na^+ in the leaves. A saline level of more than 0.25 M NaCl damages maize plants and may stunt growth and cause severe wilting [9].

2. Salinity stress

Sodium is the main toxic ion interfering with potassium uptake and thus disturbs stomatal undulations causing severe water loss and necrosis in maize; a reduction in potassium content in the leaf symplast of maize has been reported under saline conditions. High osmotic stress due to low external water potential, ion toxicity by sodium and/or chloride, and imbalanced nutrition due to interference with the uptake and transport of essential nutrients are three potential effects of salt stress on crop growth. The latter may not have an immediate effect because plants have some nutrient reserves which can be remobilized [10, 11]. Osmotic stress is linked to ion accumulation in the soil solution, whereas nutritional imbalance and specific ion effects are connected to ion buildup, mainly sodium and chloride, to toxic levels which interferes with the availability of other essential elements such as calcium and potassium [12]. Toxic levels of sodium in plant organs damage biological membranes and subcellular organelles, reducing growth and causing abnormal development before plant mortality [13, 14]. Several physiological processes such as photosynthesis, respiration, starch metabolism, and nitrogen fixation are also affected under saline conditions, leading to losses in crop productivity.

Moreover, salt stress also induces oxidative damage to plant cells with overproduction of reactive oxygen species in maize [15]. The ability of plants to survive and produce harvestable yields under salt stress is called salt resistance. Salt resistance is a complex phenomenon, and plants manifest a variety of adaptations at subcellular, cellular, and organ levels such as stomatal regulation, ion homeostasis, hormonal balance, activation of the antioxidant defense system, osmotic adjustment, and maintenance of tissue water status to grow successfully under salinity [16–20]. An integrated approach encompassing conventional breeding together with marker-assisted selection, biotechnology, exogenous use of growth regulators/osmoprotectants, and nutrient management may be needed for successful maize cultivation on salt-affected soils [21–23].

3. The response of salinity stress on maize plant physiology

Salt stress affects the growth and development of maize; however, the response of plants varies with the degree of stress and crop growth stage. Short-term exposure of maize plants to salt stress influences plant growth, owing to osmotic stress in the first phase of salt stress without reaching toxic sodium concentrations.

3.1 Salinity stress response on seed germination

Seed germination is the most critical stage in a seedling establishment which determines the success of crop production on salt-affected soils. Generally, salt stress during germination delays the start, reduces the rate, and enhances the dispersion of germination events [23–25]. It is important to note that germination and early seedling growth are more sensitive to salinity than later developmental stages [26]. Salt stress influences seed germination primarily by sufficiently lowering the osmotic potential of the soil solution to retard water absorption by seeds, by causing sodium and/or chloride toxicity to the embryo or by altering protein synthesis. Hyper-osmotic stress and toxic effects of sodium and chloride ions on germinating seeds in a saline environment may delay or inhibit germination [25, 27]. However, in maize, it is sodium toxicity and not chloride toxicity that is the major problem in the second phase of salt stress.

3.2 Salinity stress response on vegetative, reproductive growth and grain yield

Although the root is the first organ exposed to salt stress, shoots are more sensitive to salt stress than roots [7]. Salinity promotes the suberization of the hypodermis and endodermis, and the Casparian strip develops closer to the root tip than in non-saline roots [28]. Salinity reduces shoot growth by suppressing leaf initiation and expansion, as well as internode growth, and by accelerating leaf abscission [29–31]. Salt stress rapidly reduces the leaf growth rate due to a reduction in the number of elongating cells and/or the rate of cell elongation. As a salt-sensitive crop, shoot growth in maize is strongly inhibited in the first phase of salt stress [32–34].

Salt stress may also displace calcium from plasma membrane binding sites, thus causing membrane leakiness as a primary cellular response to salt stress [35]. However, it is interesting to note that if salt stress influences the integrity of the plasma membrane, then the cell wall acidification process, which is partially dependent on adenosine triphosphate-driven outward pumping of protons across the intact plasma membrane, may also be affected [36]. Acidification of the apoplast is the major requirement for increasing cell wall extensibility, which controls extension growth [37]. In this regard, cell wall proteins such as expansions are of great interest. Expansions, wall-loosening enzymes located within the apoplast of the elongation zone of leaves [38], regulate cell elongation. The assimilate supply to growing tissues is not limited during the first phase of salt stress [39], suggesting that photosynthesis is not responsible for any growth reduction in maize during this phase. Salinity-induced growth reduction in maize is caused by suppressed leaf initiation, expansion, and internode growth and by increased leaf abscission. In maize, suppression of expansion growth by salinity is principally caused by reduced apoplastic acidification and activity of wall-loosening enzymes.

In salt-affected soils, excessive buildup of sodium and chloride ions in the rhizosphere leads to severe nutritional imbalances in maize due to strong interference of these ions with other essential mineral elements such as potassium, calcium, nitrogen, phosphorus, magnesium, iron, manganese, copper, and zinc [40, 41]. Generally, salt stress reduces the uptake of nitrogen, potassium, calcium, magnesium, and iron [42]. For maize, sodium is the principal toxic ion interfering with potassium uptake and transport, leading to disturbance in stomatal modulations and causing water loss and necrosis. Competition between potassium and sodium under salt stress severely reduces potassium content in both leaves and roots of maize [19] and reduces potassium content by up to 64% in the symplast of expanding tissues under salt stress. Moreover, salt stress not only reduces potassium uptake rates but, to a greater extent, disturbs potassium translocation from root to shoot tissues in maize, leading to lower potassium shoot contents than root contents. Reduced leaf expansion with reduced calcium contents in expanding shoot tissues in maize is due to reduced transport in a saline environment; some calcium is required to uphold cell membrane integrity for proper functioning [43]. The high values for sodium/potassium, sodium/calcium, and sodium/magnesium ratios in the total plant and apoplast and symplast of expanding tissues in maize confirm that impaired transport of potassium, calcium, and magnesium by sodium might upset plant metabolism, leading to reduced growth under saline conditions. Besides potassium and calcium, nitrogen uptake and translocation are severely inhibited under salt stress, leading to reduced nitrogen contents in different maize tissues [41, 44]. Higher buildup of sodium and chloride concentrations in different plant tissues is the principal reason for nutritional imbalances. Accumulation of high sodium and chloride ions, due to salinity, in the rhizosphere decreases plant uptake of nitrogen, potassium, calcium, magnesium, and iron and thus causes severe nutritional imbalances in maize.

Carbon fixation in maize is very sensitive to salt stress [45]. Reduced stomatal conductance, impaired activities of carbon fixation enzymes, reduced photosynthetic pigments, and destruction of photosynthetic apparatus are among the key factors limiting carbon fixation capacity of maize plants under salt stress [31, 46]. Total photosynthesis decreases due to inhibited leaf development and expansion as well as early leaf abscission, and as salt stress is prolonged, ion toxicity, membrane disruption, and complete stomatal closure become the prime factors responsible for photosynthetic inhibition. Salt stress affects stomatal conductance immediately due to perturbed water relations and shortly afterward due to the local synthesis of abscisic acid. Gas exchange analysis confirmed that reductions in net photosynthetic rates are connected with the limited availability of intercellular carbon dioxide due to reduced rates of transpiration and stomatal conductance in salt-treated maize plants.

Salt stress in maize, during the reproductive phase, decreases grain weight and number, resulting in substantial reductions in grain yield [47, 48]. Salinity-induced reductions in photosynthesis and sink limitations are the major causes of poor kernel settings and reduced grain number [49]. Salinity-induced reductions in assimilate translocation, from source to developing grains, are also responsible for poor grain setting and filling and ultimately grain yield [50].

4. Mechanisms of salt tolerance in maize

Maize plants undergo a variety of adaptations at subcellular, cellular, and organ levels to grow successfully under salinity. Salt tolerance is a complex phenomenon; maize plants manifest several adaptations such as stomatal regulation, changes in hormonal balance, activation of the antioxidant defense system, osmotic adjustment, maintenance of tissue water contents, and various mechanisms of toxic ion exclusion under salt stress.

Osmotic adjustment or osmoregulation is the key adaptation of plants at the cellular level to minimize the effects of salinity-induced drought stress, especially during the first phase of salt stress. Osmoregulation is primarily met with the accretion of organic and inorganic solutes under salinity and/or drought to lower water potential without lessening actual water contents [51]. Soluble sugars, sugar alcohols, proline, glycine betaine, organic acids, and trehalose are among the major osmolytes. Proline and glycine betaine are the major osmolytes responsible for osmoregulation in maize under salt stress. Physiologically, the exclusion of excessive salt is an adaptive trait of plants to acquire salt resistance. Accumulation of sodium in excessive amounts is highly toxic for maize growth due to its strong interference with potassium, leading to disturbed stomatal regulation. Therefore, the exclusion of excessive sodium or its compartmentation into vacuoles through tonoplast hydrogen/sodium antiporters driven by the proton gradient is an important adaptive strategy for plants under salt stress. Through this strategy, maize plants not only evade the cytosol from the toxic effects of excessive sodium and gain tissue resistance for sodium but also significantly lower the osmotic potential which contributes to osmoregulation. In root cells of maize, shifting sodium into vacuoles through the tonoplast appears to be a viable strategy to minimize sodium transport to developing shoots [16]. Absorption of excessive sodium from xylem by parenchyma cells in the xylem to limit sodium translocation to shoots is also reported in maize [52]. However, salt tolerance in maize is not linked to sodium content in shoots, but rather the ability of cells to shift excessive sodium in vacuoles to maintain low sodium concentrations in the cytoplasm seemed more important [53].

Salt tolerance in maize is also linked with higher potassium and lower sodium and chloride fluxes and cytoplasmic contents and their ability to rule out sodium and chloride from leaves to sustain a higher potassium/sodium ratio. Moreover, shifting sodium and chloride in the stems and/or leaf sheaths to lessen the buildup of toxic ions in more sensitive leaf blades is another adaptive strategy of maize plants in a saline environment [54].

Salinity-induced osmotic effects alter general metabolic processes and enzymatic activities, leading to over-generation of reactive oxygen species which causes oxidative stress in maize. Overproduction of reactive oxygen species is highly toxic and damages proteins, lipids, carbohydrates, and deoxyribonucleic acid. Photosystems I and II in chloroplasts and complex I, ubiquinone, and complex III of the electron transport chain in mitochondria are key sites for reactive oxygen species synthesis [55]. Plants have multigenic responses against salt stress that involve both osmotic and ionic homeostasis, as well as cell detoxification, which is primarily met by antioxidant defense mechanisms [56, 57]. The better leaf growth, leaf water content, and membrane stability index observed in salt-tolerant maize were associated with higher antioxidant activity with greater accumulation of polyphenols under saline conditions [19]. Catalase, ascorbate peroxidase, and guaiacol peroxidase enzymes in combination with superoxide dismutase have the greatest hydrogen peroxide scavenger activity in both leaves and roots of salt-stressed maize plants [15].

Plant growth and development is governed by the synthesis of hormones with small amounts sufficient to regulate plant growth. Auxins, gibberellins, cytokinins, ethylene, and abscisic acid are the most important phytohormones; among them, the first three are growth promoters, while the other two are growth retardants. Maize plants under salt stress make certain modifications to the synthesis of these growth substances. In a saline environment, root tips are the first to sense impaired water availability due to the osmotic effect, sending a signal to shoots to adjust whole plant metabolism [18]. Higher abscisic acid levels in salt-tolerant maize help to minimize water loss and may even regulate growth promotion. Leaf growth sensitivity decreases as abscisic acid levels increase under such conditions.

Maize plants facing salt stress undergo a variety of adaptive mechanisms at the molecular level to counteract the damaging effects of salinity stress. Of these, accumulation or inhibition of several proteins and the upregulation and downregulation of many gene transcripts are important [58]. Expression of antioxidant defense genes is triggered in maize to protect the cells from salinity-induced oxidative damage. In photosynthesizing shoots of maize, catalase activity increased due to the induction of mRNA accumulation in response to higher reactive oxygen species levels under salt stress. Likewise, the buildup of superoxide dismutase transcripts increased without any notable change in total superoxide dismutase enzymatic activity or isozyme profiles [9]. The alteration/adaptation in cell wall chemical composition may also contribute to salt resistance in maize, as a low accumulation of non-methylated uronic acid in leaf cell walls may contribute to salt resistance in the first phase of salt stress [59].

5. Management strategies

Remediation of salt affected areas with low cost, efficient, and adaptable methods is a challenging goal for scientists [11]. Different practices are used to improve growth and tolerance of crops in salt-affected areas.

5.1 Agronomic approaches (soil amendments)

For saline soil management, many chemicals and organic amendments are applied to combat the adverse effect of salinity in maize crops. Chemicals mostly applied to soil for maize crops include silicon, salicylic acid, potassium, phosphorus, gypsum, biochar, and boron, and many organic amendments are also applied. Silicon application and an increase in their availability reduce the changes caused by salinity in plants by altering the plant and soil factors [60]. Silicon application increases the photosynthetic apparatus efficiency of maize plants under salinity stress by improving and maintaining the continuity of the electron transport chain [61] Silicon is recognized as a resistance improver against salinity in the maize crop. Silicon application lessened both oxidative and osmotic stress in maize crops by improving the defensive machinery performance under salinity stress. Silicon also improved water-use efficiency. Silicon-treated maize plants showed better survival under saline conditions, and their biochemical and photosynthetic apparatus was better working than silicon non-treated plants [62]. The application of brackish water is also reported in maize plants to reclaim salt effects. Brackish water irrigation boosted K uptake and retarded Na uptake in some maize genotypes. Selection of tolerant genotypes for growing in salt affected areas would be a better reclamation method [63]. Boron is an important element for many biochemical and physiological reactions of plants [64]. Boron application alleviated the negative effect of sodium chloride-induced salinity in sweet corn. Boron improved potassium concentration and maintained membrane integrity [65]. Combined application of silicon and boron also proved effective in alleviating the salinity effect on maize crops. They both in combination enhanced maize plant physical and biological parameters and also increased total soluble sugars and proline content [66]. In saline conditions, sodium concentration increased that caused an imbalance in sodium to potassium ratio. Application of potassium maintained or lowered this ratio and alleviates the deleterious effects of sodium. Potassium application to maize crop grown in saline soil decreased sodium percentage and enhanced potassium percentage in maize grain and stalk as well as distinctly boosted the maize salt tolerance by decreasing the sodium to potassium ratio. The most significant effect was observed at higher potassium fertilizer application rates [67].

Combined application of potassium sulfate and diammonium phosphate on maize in saline soil for maize (*Zea mays* L.) showed that maize responded well to potassium and phosphorus fertilization. Salinity effects were amended by potassium and phosphorus fertilizer application and improved yield. The influence of potassium was great on grain yield compared to phosphorus. K affected yield-related parameters, and phosphorus showed substantial effects on sodium, potassium, magnesium, and sodium to potassium ratio. Potassium application decreased sodium concentration and ultimately decreased sodium to potassium ratio [68]. Foliar application of potassium chloride, boron, and thidiazuron was done on maize crops in saline stress. Thidiazuron and potassium application improved the physiological parameters of the crop. Thidiazuron proved more efficient in alleviating the adverse effects of salinity than potassium and boron. Potassium content, chlorophyll content, total carbohydrate protein percentage, and total soluble salt percentage were substantially improved by foliar application of thidiazuron; however, transpiration rate and proline content were decreased [69].

Flue gas desulfurization gypsum (FGDG) application can reduce sodium toxicity by replacing it with calcium at the cation exchange site and results in increased clay particle flocculation near the surface of the soil [70]. Furfural residue is rich in organic carbon and can increase the SOC content, reduce soil bulk density, and lower soil pH [71]. Flue gas desulfurization gypsum and furfural residue combined application reduced the yield gap of maize and recovered soil properties. Flue gas desulfurization gypsum and furfural residue increased the organic carbon (SOC) and calcium contents and decreased the upper soil layer pH and sodium content. Mineral nutrients like phosphorus, nitrogen, potassium, magnesium, and calcium accumulations in maize increased significantly, and sodium accumulation decreased in the flue gas desulfurization gypsum and furfural residue treatment compared with control [72].

Hydrogen peroxide as foliar spray effectively curtailed the effects induced by salinity because of increased antioxidant enzyme activities: ascorbate peroxidase, guaiacol peroxidase, superoxide dismutase, and the most responsive catalase [73].

Salicylic acid is an imperative secondary metabolite that is used in salinity management as it induces resistance against salinity in plants by regulating physiological processes through signaling. Maize plants exposed to sodium chloride induced salinity, reduced plant dry biomass, increased membrane permeability, and reduced nutrient availability, while those plants supplied with exogenous salicylic acid increased dry biomass, decreased membrane permeability and lipid peroxidation, and increased iron, zinc, copper, and manganese contents. Salicylic acid application further improved nutrient uptake by maize plants except for zinc in the saline condition. Salicylic acid reduced chloride and sodium accumulation considerably [22].

In another study, a maize crop dry weight and leaf area decreased by 51.43 and 53.18%, respectively, when irrigated with saline water, while salicylic acid foliar application at the rate of 200 ppm remedied the harmful salinity effects and improved whole plant dry weights and leaf area and improved proline and amino acid contents such as lysine, arginine, glutamic acid, and serine accumulation under saline stress conditions [74].

Organic amendments proved as an effective strategy for saline soil amelioration. Organic amendments improve soil chemical and physical properties. Solid waste, vermicompost, and cow dung influence soil salinity and alleviate its adverse effects on the growth of plants by changing the physico-chemical properties of soil. Solid waste, vermicompost, and cow dung reduced soil electrical conductivity as well as improved shoot and root length [75].

Compost and vermicompost application increased maize plant dry matter and plant height and reduced soil pH and electrical conductivity. Extractable phosphorus, total nitrogen, soil organic carbon, cation exchange capacity, and potassium, calcium, and magnesium concentrations were improved by the application of vermicompost and compost. Sodium concentration decreased because of its replacement by calcium ions and then leaching. This results in a decrease in soil salinity levels [76].

Biochar also improved physico-chemical properties of soil, including soil cation exchange capacity, pH, water holding capacity, surface area, and soil structure under abiotic stresses [77]. Biochar application improved potassium availability uptake and decreased sodium availability and uptake under salt stress [78, 79]. Biochar made by cow manure is a rich source of many plant nutrients which significantly increased nutrient uptake in maize crop. Cow manure biochar application improved net WUE, field-saturated hydraulic conductivity, and significantly increased Oslen-P, total N, pH, total C, exchangeable cations, and cation exchange capacity [80]. Compost manure and crop straw biochar and pyroligneous solution can improve maize productivity and combat salinity stress. Compost manure and crop straw biochar both increased nutrient statuses and decreased salinity by reducing chloride and sodium accumulation and increasing potassium concentration. Manures also increased plant performance, maize grain yield, and leaf area index, with a decrease in electrolyte leakage. Leaf bioactivity associated with osmotic stress was improved significantly [81]. It is concluded that exogenously applied organic matters such as plant residues, manure, a by-product of municipal or farming activities, etc. are an efficient and feasible way to mitigate the effects of salinity on plant growth and soil health. Organic amendments at optimal rates (>50 tons per hectare) can improve soil chemical like cation exchangeable capacity, pH, etc. and physical properties like permeability, soil structure, water holding capacity, etc., approving maize plant growth [82].

5.2 Application of hormones

Hormones govern many processes inside plants that regulate plant growth: auxins, gibberellins, and cytokinins are growth promoter hormones, while abscisic acid and ethylene are the growth retardants. Under salt stress conditions, growth-promoting hormones are applied exogenously to overcome the adverse effects of salinity on maize plant growth and development.

Cytokinin is a plant growth regulator that plays a vital role in cytokinin-dependent processes that regulate plant adaptation, growth, and development processes [83]. It is reported in recent research that cytokinins of developing maize seeds may come from both transport and local synthesis. Cytokinin fertilization at higher rates suggested parental control on plant metabolism [84]. Cytokinin and auxin application alone or in combination with maize plants reduced the deleterious effect of salinity on plant growth and increased physical parameters like stem diameter, plant height, ear length, row number per ear, and biological yield like grain yield and number at different concentrations. A single application of cytokinin played a role in improving kernel number per row, while a single application of auxin increased grain weight and better harvest index in saline condition [85].

Kinetin is one form of cytokinins and is known to boost the crop plant growth grown under saline conditions [86]. Kinetin and indoleacetic acid (auxin) applications as foliar spray overcame to adversative effects of sodium chloride induced stress on physiological parameters at the earlier stages of maize plants at a variable extent. Foliar combined application of both kinetin and indoleacetic acid substantially increased K^+ and Ca^{2+} concentration and reduced those of Na^+. Their application also increased essential inorganic nutrients and maintained membrane permeability and in result thwarted some salt-persuaded adversative effects [19]. Exogenous combined application of inorganic nutrients and indoleacetic acid improved phosphorus, calcium, and magnesium contents and decreased sodium concentration in maize plants grown in saline condition. Improvement in growth by indoleacetic acid and organic nutrient application is linked with an improved concentration of photosynthetic pigment, more leaf sodium to potassium ratio, rehabilitated activities of some antioxidant enzymes such as CAT and SOD, and reduced membrane permeability under salinity. Exogenous foliar application of indoleacetic acid additionally improved the CAT and SOD activities in salt-stressed maize plants, while increasing effect was not detected in activities of POX or PPO [87]. Previously, foliar application of indoleacetic acid enhanced the essential nutrient uptake along with a noteworthy decrease in sodium uptake that resulted in better growth and yield of maize plant under salt stress condition [88].

The combined application of sodium chloride-induced salinity and gibberellic acid on maize plant growth and nutritional status was studied. Salinity decreased chlorophyll content, total dry matter, and relative water content, whereas increased enzyme activities peroxidase polyphenol oxidase superoxide dismutase and proline accumulation. Gibberellic acid overcame the deleterious effects of sodium chloride-induced salinity stress on the above physiological characteristics to a variable extent. Gibberellic acid decreased enzyme activities and increased physiological parameters and macro- and micronutrient concentration. Foliar application of gibberellic acid counteracted some salinity adverse effects by the buildup of proline concentration which sustained membrane permeability [89]. A comparison between gibberellic acid and salicylic acid under the saline condition in maize plant showed that gibberellic acid was more efficient in resisting salinity effect on leaves than salicylic acid. Gibberellic acid also improved the nutrient status of plant except for copper and manganese [90].

5.3 Application of PGPR

Soil has an enormous microbial versatility that belongs to different groups of fungi, Archaea, and bacteria [91]. Microorganisms are used in agricultural fields, and they can lessen many abiotic stresses [92, 93]. Usually, bacteria are used for promoting plant growth and alleviating many abiotic stresses. These bacteria are usually termed as plant growth-promoting rhizobacteria (PGPR). PGPR is rhizospheric or endophytic bacteria that colonize the root either interiorly or exteriorly. Bacterial genera such as *Achromobacter*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Methylobacterium*, *Microbacterium*, *Paenibacillus*, *Pantoea*, *Pseudomonas*, *Rhizobium*, *Variovorax*, etc. provide tolerance to host plants against abiotic stresses [94, 95]. Stress tolerance is boosted by microbes by various mechanisms and production of indoleacetic acid, gibberellins, and many other elements. These elements improved the root growth and enhance nutrient content, thus improving the plant health under salt stress [95]. Bacteria that help plants in alleviating salt stress are called halotolerant or salt-tolerant or salt-loving bacteria. These halotolerant microbes have vital importance in the field of agriculture. In arid and semi-arid regions, they improve crop productivity [91]. Specific PGPR inoculations help to boost salt stress tolerance in plants by induced systemic tolerance (IST). Induced systemic tolerance changes many biochemical and functional characteristics. The PGPR improves salinity tolerance by either direct mechanism (indoleacetic acid (IAA) synthesis phosphate solubilization, nitrogen fixation, etc.) or indirect mechanism (exopolysaccharides (EPS), antioxidant defense, osmotic balance, and volatile organic compounds (VOCs)) and improves plant growth [96] (**Table 1**).

5.3.1 Osmotic adjustment

Osmotic adjustment is the maintenance of cell turgidity by increasing compatible solutes, vital for regular cell functioning. Compatible solutes decrease osmotic stress caused by salts [55]. PGPR produce and secrete compatible osmolytes to mitigate the harmful effect of salts and help plants improve their growth. Proline is the main osmolytes in reducing osmotic stress and produced by the hydrolysis of proteins in the plant. Under salt stress, glycine betaine and proline are usually produced and accumulated in plants. There is a dearth of organic osmolytes production such as trehalose in plants [112]. Under salinity, proline plays a multifunctional role like regulating cytosolic acidity, protein maintenance, ROS

PGPR strain	Mechanism	Improvement in crop	References
Pseudomonas syringae, *P. fluorescens*	ACC deaminase	Improved plant growth	[97–100]
Pseudomonas spp.	EPS		[101]
P. aeruginosa	IAA production, ACC deaminase, phosphate solubilization, and biofilm formation		[102]
Pseudomonas spp.	Osmotic regulation		[103]
Proteus penneri	EPS		[101]
Pantoea agglomerans, *Staphylococcus sciuri*, *Arthrobacter pascens*	Upregulation of aquaporin genes		[94, 104, 105]
Gracilibacillus, *Staphylococcus*, *Virgibacillus*, *Salinicoccus*, *Zhihengliuella*, *Brevibacterium*, *Oceanobacillus*, *Exiguobacterium*, *Arthrobacter*, and *Halomonas* spp.	Antioxidant enzyme phosphate solubilization, osmotic regulation and antioxidant enzymes IAA production, ACC deaminase, phosphate solubilization, and biofilm formation		[102]
Serratia liquefaciens KM4	Facilitated gas exchange, osmoregulation, antioxidant enzymes, nutrient uptake, and downregulation of ABA biosynthesis		[106]
Enterobacter aerogenes, *Enterobacter* spp.	ACC deaminase	Reduced ethylene production	[97, 98]
Azospirillum brasilense	Ion toxicity, NOR, and nitrogenase activity	Improved chlorophyll content Improved nutrition	[100]
A. faecalis, *A. brasilense* strains Ab-V5 and Ab-V6	EPS, antioxidant enzymes, and proline contents		[101, 107]
Azotobacter chroococcum	Improved K/Na ratio, polyphenol content, and proline concentration		[108]
B. amyloliquefaciens	Soluble sugar content and antioxidant enzymes	Improved plant growth and photosynthetic rate	[109]
Bacillus spp.	Phosphate solubilization, osmotic regulation, and antioxidant enzymes		[104]
Bacillus aquimaris	Chlorophyll content, osmotic regulation, and antioxidant enzymes		[110]
Bacillus	IAA production, ACC deaminase, phosphate solubilization, and biofilm formation		[102]
Geobacillus sp.	Increased proline content		[111]
Rhizobium	Osmotic regulation	Increased chlorophyll and photosynthesis rate	[103]
Rhizobium tropici strain CIAT 899	Antioxidant enzymes and proline contents		[107]

Table 1.
PGPR and their mechanisms for salt tolerance.

scavenging decrease in peroxidation of lipids, etc. PGPR inoculation in plants showed improved proline levels under salt stress. *Arthrobacter pascens* inoculation produces more proline in corn plants [104]. *Pseudomonas* spp. improved growth of maize plant by production of proline that helps in osmotic adjustments [103]. *Azotobacter chroococcum* improved nutrition [108], *Geobacillus* sp. increased photosynthetic rate [111], and *Rhizobium* spp., *Rhizobium tropici* strain CIAT, *A. brasilense* strains Ab-V5 and Ab-V6 [107], and *A. faecalis* [101] enhanced chlorophyll content and photosynthetic rate by increased accumulation of proline and osmotic adjustments in maize plants.

5.3.2 Antioxidants

Plants normally produce reactive oxygen species during cellular metabolism in less quantity. However, under salinity stress conditions, increased production of reactive oxygen species occurs, which alters redox state, denatures membrane bound proteins, reduces fluidity of membrane, causes DNA damage, destroys enzymatic actions, changes formation of protein, and destroys cell homeostasis, which can damage the cell and finally cause cell death [113]. PGPR excrete many enzymatic antioxidants (ascorbate peroxidase (APX), catalase (CAT) dehydroascorbate reductase, glutathione reductase (GR), superoxide dismutase (SOD), non-enzymatic antioxidants, ascorbate, tocopherols, glutathione, and cysteine) [114]. *Staphylococcus sciuri* induction induces more antioxidant production in maize plants that helped in the degradation of reactive oxygen species and improved plant growth [94]. *A. faecalis* [101], *Serratia liquefaciens* KM4 [106], and *Bacillus* sp. [104] are reported to increased maize growth, nutrition, and photosynthetic rate by producing more antioxidative enzymes. *Azotobacter vinelandii*, *Pseudomonas fluorescens*, and *Pseudomonas putida* restored lipids and antioxidant enzymes peroxidase and catalase to semi-normal levels under saline condition [115].

5.3.3 Exopolysaccharides

PGPR produce exopolysaccharides (EPS), which are either homo- or heteropolysaccharides. These EPS bind to the cell surface like a capsule and make a biofilm [116]. Different microbes produce different types of polysaccharides, but some common monomers comprise glucose, galactose, and mannose. Uronic acids (fucose and rhamnose), amino sugars (N-acetylamino sugars), neutral sugars (galacturonic), pyruvate ketals, and ester-linked substituents are EPS constituents [117]. PGPR produce EPS and form hydrophilic biofilms under saline conditions and improve plant growth significantly [118]. EPS producing PGPR makes rhizosheaths around roots that help fight against salt stress by attaching Na^+ ions with EPS. Attachment of Na^+ ions to EPS decreases the toxicity of Na^+ and makes it inaccessible for plants [119]. *P. aeruginosa* improved plant growth because of more EPS content production. *Pseudomonas* spp. produced more EPS and increased root growth and nutrition in maize plants [101]. Many other PGPRs such as *Gracilibacillus*, *Salinicoccus*, *Staphylococcus*, *Zhihengliuella*, *Bacillus*, *Brevibacterium*, *Virgibacillus*, *Oceanobacillus*, *Arthrobacter*, *Exiguobacterium*, and *Halomonas* spp. are reported to improve maize growth by the formation of biofilm [102]. *B. amyloliquefaciens* improved plant growth by the accumulation of soluble sugar content [109].

5.3.4 Volatile organic carbons

Rhizobacteria that produce lipophilic fluids with high vapor pressures are called volatile organic compounds. They communicate by cell signaling between organisms to improve growth. The VOCs are species-specific and promote the biosynthesis of glycine betaine and choline. These osmolytes improve plant tolerance against osmotic stress. A high level of VOCs in plants is a sign of activated self-protective response against salt stress [120].

The VOCs produced by *Bacillus subtilis* triggered the gene of HKT1/K^+ transporter and inhibited sodium ion influx through roots and eliminated salt stress. It also encouraged the glycine betaine synthesis that decreased the uptake of Na^+ through roots and transported more nutrients toward shoot than during salt stress [120].

5.4 Seed priming

Poor crop stands because of low seed germination rate in salt-affected areas are a challenge for the lucrative production of a crop. Maize seed germination rate is affected by toxic effects of chloride and sodium ions [25]. Seed priming helps to recover maize germination rate in salt-affected areas. Seed priming is a pre-sowing treatment either with water or any chemical of interest that boosts seed performance with a quicker and harmonized germination under sub-optimal and optimal conditions [121]. This is a physiological treatment under salinity in which seeds are moderately hydrated and radicle does not emerge [122]. Priming treatments include hydropriming with water, osmopriming with salts or osmolytes, and hormonal priming with hormones. Partial hydration is enough for the physiological process occurrence that is typical of the first stages of imbibition (pre-germinative metabolism) [123]. Under saline conditions germination rate improved by soaking maize seeds in water priming with water under salinity-enhanced maize seedling vigor index, germination index, final germination percentage, and seedling length, showing its potential as a seed invigoration technique under salinity for better maize performance [23].

Priming of seeds with salt solution enables them to break their dormancy and escape from disease-causing agents and competent seeds of weeds [124]. Priming seeds with NaCl significantly enhanced maize plant growth. Fresh and dry weights of roots and shoots were increased. Under salt stress, seed priming lessened the inhibitory effect of salt stress on maize seedling growth [125]. Priming with NaCl also increased plant height and yield and induced early emergence, more germination rate, more shoot length and dry weight, and more leaf chlorophyll, area, and number [126]. Seed halopriming with calcium chloride, sodium chloride, and potassium chloride was effective in mitigating the salt adversities on maize seed germination. Calcium chloride priming was most operative. Calcium, sodium, and potassium concentrations improved significantly in all parts of germinating seed. Most of the calcium was reserved in mesocotyl and seed, thus limiting its transference to radicles and plumules.

Seed priming with NaCl and $CaCl_2$ had significant effects on germination rate, earlier growth, number of branches, cobs number, and yield. This increase in growth traits likely helps to reduce the competition for water and nutrients with associated improvements in seed yield. Sodium chloride seed priming increased shoot length, and calcium chloride seed priming increased root length. In vertisol soil, seed priming is preferred for improved crop yield and stand establishment, while in lithosol soils, seed priming is preferred for well germination of seed and increased cob number [124].

Other priming agents include thiamin, pyridoxine, and ascorbic acid, which not only improved the germination of pretreated seed but also improved seed growth and yield under salinity. Enhanced maize seedling biomass under saline conditions is reported by hormonal priming with chloro-ethyl-phosphonic acid, an ethylene releaser [127]. Salicylic acid application under saline conditions at the rate of 0.1 mM enhanced growth and development of plants [128]. Priming with 28-homo-brassinolide improved the antioxidative enzyme activities and lowered lipid peroxidation and increased concentration of protein, thus signifying that

28-homo-brassinolide can lessen oxidative stress in salt-affected maize plants [129]. Priming with hydrogen peroxide improved activities of catalase ascorbate peroxidase and guaiacol peroxidase and increased seed germination percentage, under salt stress condition in maize plants [73].

Seeds of maize hybrid FH-810 were soaked in water (hydropriming), calcium chloride (2.2%, osmopriming), *Moringa* leaf extracts (MLE 3.3%, osmopriming), and salicylic acid (SA, 50 mg L^{-1}, hormonal priming), each for 18 h. Plant length, biological yield, 1000-grain weight, and harvest index were improved by seed priming. However, osmopriming with MLE and hormonal priming were more effective in these parameters. Hormonal priming at seedling stage increased the leaf chlorophyll contents and decreased the electrical conductivity followed by osmopriming with CaCl2. Hormonal or osmopriming with MLE improved the yield performance at early planting primarily by increased crop growth, net assimilation rates, a leaf area index, and maintenance of green leaf area at maturity. Hormonal priming with SA and osmopriming with MLE were the most economical methods in enlightening early planted spring maize productivity by early seedling growth stimulation at low temperature [130].

5.5 Application of molecular and genetic approaches such as MAS, selection, and breeding approaches

Maize is a polymorphic plant because of its cross-pollinated nature and genetic variations for salinity resistance. It is commonly a moderately salt-sensitive crop, but some salinity tolerant genotypes also exist. Tolerance in these genotypes occurs because of higher potassium and lower chloride and sodium cytoplasmic contents. Mass screening of maize genotypes is done to identify and isolate salt-tolerant germplasm for breeding purposes and to develop better performing genotypes. Screenings for salt tolerance or resistance are usually done at the early growth stages of maize plants [21]. Many plant characteristics are identified as salt-tolerant traits. Acidification of cell wall because of better H^+-ATPase activity in the plasma membrane in salt-tolerant maize hybrid (SR 03) appeared as an important tolerance/resistance trait. Turgor, cell wall acidification, and osmotic adjustment, in newly established salt-resistant maize hybrids, are a salt-resistant trait [48]. More abscisic acid accumulation in salt-resistant genotypes plays a role in osmotic adjustments under saline condition [39]. Salt-tolerant genotypes usually had lower sodium accumulation and more potassium to sodium and calcium to sodium ratio. Sensitive genotypes had more sodium accumulation, suggesting that accumulation of sodium in shoots is a reliable screening parameter for salt tolerance/resistance in maize at early stages of growth [21]. However, higher sodium accumulation was observed in salt-tolerant Giza 2 roots than in salt-sensitive Trihybrid 321. Many other traits of maize plants such as growth rate, seedling weight, and photochemical efficiency should also be used for screening and breeding of salt-tolerant crops [131].

A proteomic approach is also used to recognize salt resistance-associated proteins in maize in breeding programs for markers to develop salt-tolerant/salt-resistant genotypes. The use of physiological and molecular markers to recognize salt-resistant genotypes of maize is a reliable approach [132]. Sodium and soluble organic solute accumulations in roots were associated with maize salt resistance. More soluble organic solute and sodium accumulation in maize salt-tolerant genotype roots (BR5033) than in salt-sensitive genotype (BR5011) was reported. Hence, soluble organic solute and sodium accumulations in roots can be used as physiological markers to screen and isolate salt-resistant maize genotypes [15]. More total separated proteins (>80%) in severe saline stress in maize genotypes and 45 and

31% increase in root and shoot proteins under mild salinity showed differential regulation of proteins [58].

Transferring one or more salt-resistant genes from one species to another to insert required quantitative and qualitative characteristics is stated as the transgenic approach. This practice is much quicker than conventional breeding practices, and it warrants wanted genes induction without the addition of excess genes from the donor organism [133]. Improvements and advances in biotechnology and functional genomics have made it feasible to identify and distinguish salinity-tolerant genes that help to develop salt-resistant plants by the use of transgenic tactics (27).

By using the Flippase recombination enzyme P/Flippase recognition target-based marker elimination system to eliminate the *als* gene [134]. Marker-free salt-tolerant transgenic maize is produced to improve the bio-safety of the environment. Under the saline condition, transgenic maize seed inserted with AtNHX1 gene and wild-type maize were planted. Wild-type maize plants withered, and upper leaves shriveled, whereas 56% of transgenic plants survived salinity up to the six-leaf stage. More grain yield, 1000-grain weight, was recorded in transgenic plants under saline condition than those under non-saline conditions. More potassium accumulation in root and shoot was observed in transgenic plants [134].

The sodium vacuolar compartmentation or cytoplasmic exclusion into the apoplasts through tonoplast sodium/hydrogen antiporters or plasma membrane is an adaptive mechanism to alleviate the adverse excess sodium effects in maize plants [26]. Under saline conditions, transgenic maize plants were better than wild-type plants because of higher hydrogen/sodium exchange rates in vesicles of tonoplast. Also, the efficient sodium vacuolar compartmentalization in cells of transgenic maize plants improved salt tolerance as well as the productivity of grain [134].

Salt stress boosted ZmNHX transcription which caused an increase in antiporters (sodium/hydrogen) of tonoplast in salt-resistant maize leaves by impounding sodium into vacuoles of the leaf to reduce sodium ion effects on the cytoplasm [135]. Transgenic maize plants with inserted sodium/hydrogen antiporter (OsNHX1) gene from *Oryza sativa* gave better yield than wild-type maize at 200 mM NaCl. Lower osmotic potential coupled with higher potassium and sodium contents in transgenic maize leaves was recorded under saline condition compared to wild maize [136].

The complementary DNA (cDNA) micro-array is an operative method for expression profile studies to assess differences and similarities under salinity stress in diverse patterns of expression. A cDNA macro-array with 190 maize expressed sequence tags persuaded by water stress was applied to cold stress, abscisic acid, and high salinity conditions. High salinity stress upregulated 41 sequence tags in roots and 36 sequence tags in leaves [137]. Quan et al. (2004) [138] introduced the betA gene encoding choline dehydrogenase (AtNHX1), which was inserted in maize line DH4866 from *Escherichia coli* to develop transgenic maize. This gene improved the biosynthesis of glycine betaine from choline under salinity and increased salt resistance in maize plants [139]. In conclusion, maize genotypes with externally inserted genes of betaine aldehyde dehydrogenase and vacuolar sodium/hydrogen antiporter, etc. performed better under salinity stress and can be used for inducing salt resistance in maize plants.

6. Conclusions

Salinity stress poses a serious threat to maize. It affects the plant physiology and reduces growth and yield. Salinity affects the maize crop at different growth stages. Seed germination is the stage that is affected adversely by salinity, and germination rate is reduced. At vegetative and reproductive stages, salinity affects photosynthesis, respiration, transpiration, stomatal and hormonal regulation, and water relation processes. These processes affect the growth pattern of plants and cause reduction in growth and yield. To mitigate the effects of salinity on maize crop, different management practices are used. Management by agronomic means, such as application of nutrients (through the application of biochar, compost, gypsum and nutrient fertilizers, etc.), either exogenously or as seed priming with different chemical and hormones, exogenous application of hormones, and growing of resistant cultivars, proved effective in reducing the adverse effects of salinity on maize crops. PGPR application mitigates the salinity stress by the production of different hormones, exopolypolysaccharides, or volatile organic compounds. Different genetic and molecular techniques are also used for inducing salinity tolerance by the insertion of tolerant genes in maize plants. For the future, more work on improved genetic and molecular techniques is needed.

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Conflict of interest

There is no conflict of interest among all the authors. All the authors revised and approved the chapter.

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